

**BIOLOGY AND IMMATURE STAGES OF *TYPOPSILOPA NIGRA* (WILLISTON)
(DIPTERA: EPHYDRIDAE), A SECONDARY CONSUMER OF DAMAGED
STEMS OF WETLAND MONOCOTS**

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Abstract.—We investigated the biology and morphology of *Typopsilopa nigra* (Williston) (Diptera: Ephydriidae) from southern California wetlands. Immatures were found as secondary invaders of stems of bulrush and cattails tunneled by larvae of the noctuid moth *Bellura obliqua gargantua* (Dyar). Adults were taken frequently from stands of California bulrush and cattails. Mating pairs exhibited tropholaxis immediately after copulation; females laid eggs on decaying plant fragments in breeding cages. Newly hatched larvae consumed decaying lettuce, bulrush, cattails, and other putrid plant materials. Development required 2–3, 2–3, and 3–4 d for instars 1–3, respectively, and the pupal period lasted 6–7 d. The microbial flora associated with decaying plant matter probably provided most of the nutrition for larval development. During a choice experiment, newly mated females were offered ovipositional substrates of decaying bulrush, cattail, sedge, buttercups, and controls (no vegetation); most eggs were laid during the first several days, and the numbers declined over time. Significantly more eggs were deposited on putrefying buttercups than all other substrates despite no evidence of this plant being used in nature. We suggest that the semi-liquid medium formed by the rotting buttercups provided a more suitable moist substrate for oviposition than the other treatments. Damaged areas of plants where the immature stages occurred were naturally quite moist. These data lead us to hypothesize that natural selection probably acted more heavily on adult ovipositional behavior than on larval trophic ecology.

Key Words: shore flies, *Typopsilopa*, secondary invader, oviposition, cattails, bulrush, Noctuidae

When plants are damaged by herbivorous insects, a niche often becomes available for saprophagous species which take advantage of decaying plant tissue and frass. The order Diptera is replete with secondary invaders, and this feeding strategy has evolved independently many times in numerous families (Ferrar 1987). Freshwater marshes frequently harbor dense stands of monocotyledon plants such as cattails (*Typha* spp.), sedges (e.g., *Carex* spp.), and grasses (e.g.,

Phalaris spp.) that are attacked by herbivorous insects and subsequently utilized by saprophagous dipterans (Claassen 1921, Cole 1931, Penko and Pratt 1987, Allen and Foote 1992). Although the secondary invaders do little or no damage to the plants they inhabit, they undoubtedly play important roles as nutrient recyclers in wetlands.

The genus *Typopsilopa* Cresson (Diptera: Ephydriidae) contains four species in North America (Mathis and Zatwarnicki 1995),

with *T. atra* (Loew) being the most common and widespread. Adults of that species have been collected in sedge meadows and the larvae reared on laboratory cultures of yeast or decaying lettuce (Deonier 1965, Scheiring and Foote 1973, Foote 1995), but biological data on other species are lacking. To our knowledge, no descriptions of the immature stages are available for *Typopsilopa*, although adults are collected frequently (Deonier 1965, Scheiring and Foote 1973, Zack 1998). *Typopsilopa nigra* (Williston) is found from Virginia to Florida west to California, and extends southward into the Neotropics (Mathis and Zatwarnicki 1995). Our studies of wetlands Diptera showed that this species was a secondary invader of monocots and was commonly collected during the summers of 1998 and 1999 in a southern California constructed wetlands. Herein, we give information on the larval feeding habits and natural history of this species, and describe the egg, three instars, and puparium. We performed an oviposition experiment to ascertain the degree of host specificity exhibited by this species.

MATERIALS AND METHODS

Adults and immature stages were collected at the Prado Constructed Wetlands near Corona (CA, Riverside Co.). This large marsh is over 120 ha in area, receives water from the Santa Ana River, and acts as a biofilter for potential drinking water for southern California. Extensive stands of cattails (*Typha* sp.) and California bulrush (*Schoenoplectus californicus* [Meyer] Sojak) dominate the floral components, although smartweeds (*Polygonum* sp.), pennywort (*Hydrocotyl* sp.), and several species of buttercups (*Ranunculus* spp.) are also common.

Adults were taken with aerial sweep nets or by aspirating resting individuals directly off plants. Immatures were found in cattail and bulrush plants whose stems exhibited feeding damage in the form of an entrance hole created by larvae of *Bellura obliqua*

gargantua (Dyar) (Lepidoptera: Noctuidae). Damaged plants were cut with shears and returned to the laboratory to collect *T. nigra* larvae and puparia for rearing. Immatures were placed in petri dishes with shredded plant material to observe larval feeding and to procure adults emerging from puparia. Dishes were kept at laboratory temperature (20–22°C) and a 16:8 light:dark photoperiod maintained with incandescent lights.

One adult female was placed in a mosquito rearing cage (BioQuip Products, California) with moist paper toweling lining the bottom. Ten cm sections of cattail stem split open with a razor to hasten decay were added to the cage. A yeast/sugar/water pellet was placed in the cage as an adult food source. We observed oviposition, and eggs were transferred daily to petri dishes lined with moist paper toweling to await eclosion. Newly hatched maggots were transferred to different petri dishes containing putrid lettuce which had been decaying under refrigeration for several months. Behavioral observations were made with a dissecting microscope.

Although we examined a variety of wetlands plants for immature stages, we found *T. nigra* immatures only in bulrush and cattail plants. To test the hypothesis that females selectively oviposit in these plants, we performed a choice experiment with adults obtained from laboratory rearings. Undamaged California bulrush, cattails, sedges (*Cyperus* sp.), and buttercups (*R. flammula* var. *ovalis* [Bigel]) were collected and homogenized in a blender. After conditioning for five days to promote decay, four petri dishes (25 mm diameter) were lined with 2–3 layers of moist unbleached paper towel and filled with one plant species; petri dishes with moist paper towel but no plant material served as controls. One of each of the treatment dishes was placed randomly in the bottoms of five mosquito breeding cages. A yeast/sugar/water pellet was attached to the wall of each cage, and a male and female *T. nigra* were added. Af-

ter 2 d, dishes were removed and the number of eggs laid on each substrate counted, removed, and placed in a new petri dish with moist paper towel. Eggs were enumerated and removed daily thereafter. Water was added to each dish as necessary to keep the substrate moist, and the material was homogenized periodically to prevent mold from engulfing the surface. A Kruskal-Wallis one-way ANOVA on ranks was calculated to compare the mean number of eggs laid on each substrate (data $\log_{10}[n+1]$ transformed).

Field-collected and laboratory-reared immature stages were fixed in KAA solution and then preserved in 70% ethanol. Tagged image format computer files of immatures were obtained with a Wild MZ-8 dissection scope and a low light camera in conjunction with an IBM personal computer. Computer images were printed on a laser jet printer and traced or used as a reference to facilitate illustration. To obtain highly magnified images, the low light camera was attached to a Leica compound microscope. Some larvae were dissected and structures of interest (spiracles, cephalopharyngeal skeletons, and integument) were placed on a microscope slide to which a drop of Canada balsam was added and covered with a coverslip.

Representative adult specimens were added to the Diptera collection of the University of California, Riverside, Entomology Research Museum.

RESULTS

Typopsilopa nigra (Williston)

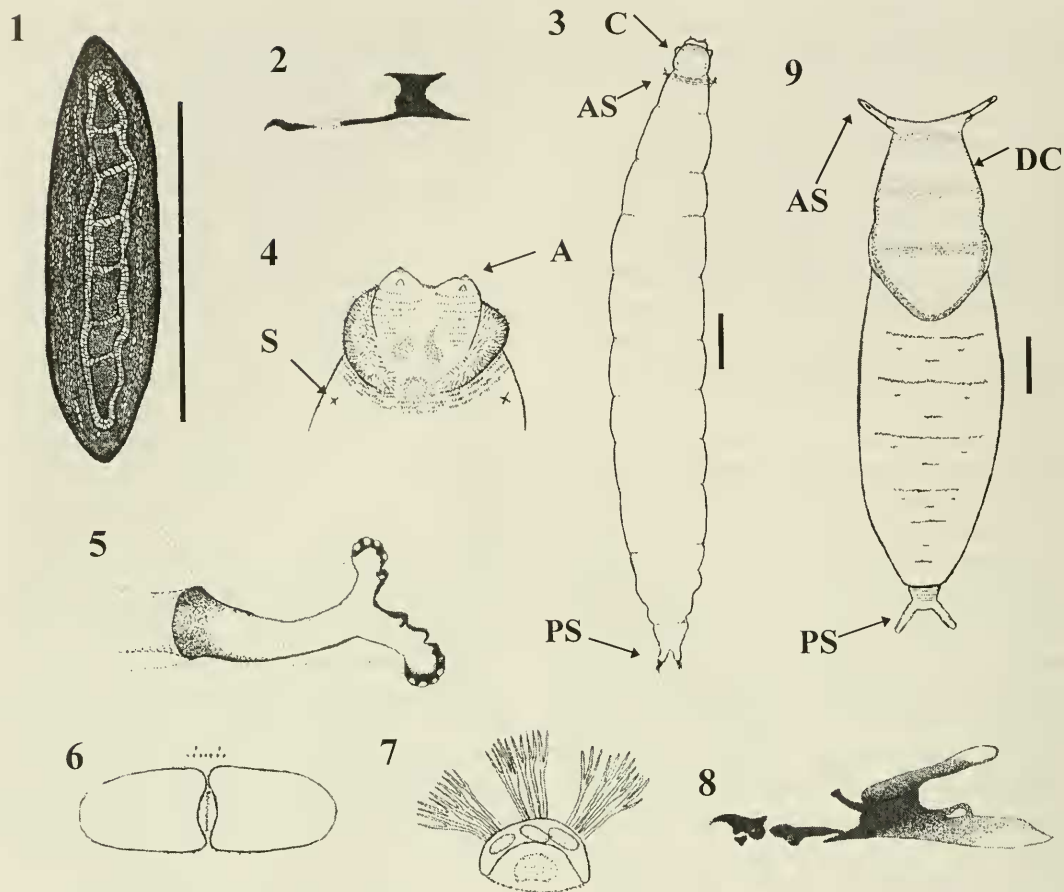
Descriptions of Immature Stages

Egg.—Length 0.76–0.88 mm ($\bar{x} = 0.81$); maximum width 0.20–0.24 mm ($\bar{x} = 0.22$) (Fig. 1). Uniformly white, elongate, ovoid, somewhat flattened dorsally. Chorion striated longitudinally, with two strong ridges dorsally, dorsal ridges connected by several perpendicular ridges; numerous fine ridges ventrally. Terminal micropyle small, inconspicuous ($n = 10$).

First instar.—Similar to third instar except for following characters. Length 1.02–1.40 mm ($\bar{x} = 1.23$); maximum width 0.18–0.28 mm ($\bar{x} = 0.22$). Cephalopharyngeal skeleton reduced, mandibles shorter, no accessory teeth (Fig. 2). Anterior spiracles absent. Perianal pad not discernible. No spines on anteroventral area of eighth abdominal segment. Only apex of respiratory tube brown, otherwise entire larva white to nearly transparent ($n = 6$).

Second instar.—Similar to third instar except for following characters. Length 1.68–2.60 mm ($\bar{x} = 2.18$); maximum width 0.26–0.40 mm ($\bar{x} = 0.32$). Anterior spiracles bifurcate with 3–4 papillae per branch. Six to eight brown spines in one row on anteroventral area of eighth abdominal segment. Posterior spiracles strongly sclerotized, brown, somewhat glabrous ($n = 9$).

Third instar.—Length 3.08–6.56 mm ($\bar{x} = 4.93$); maximum width 0.50–1.02 mm ($\bar{x} = 0.76$). Elongate muscoid, uniformly white, integument somewhat transparent showing yellowish fat bodies anteriorly in live specimens. Abdominal segments parallel sided, tapering to breathing tube posteriorly, thoracic segments tapering anteriorly (Fig. 3). Cephalic segment bilobed apically, with short two-segmented antenna dorsally, maxillary palp ventrally; facial mask with eight rows of small spines directed posteriad, triangular at high magnification (Fig. 4). Sensillum scattered, four branched (Fig. 4). Anterior spiracles retractile, bifurcate, with 5–7 papillae per branch; papillae round with dark border in lateral view (Fig. 5). Abdominal segments not well defined; venter of each segment with area of small spines forming poorly delimited creeping welt. Eighth abdominal segment with 12–14 small black spines anteroventrally positioned in two relatively even rows. Perianal pad slightly swollen, somewhat darker than rest of abdomen, each half truncate mesad and evenly rounded laterad, divided by anal slit (Fig. 6). Breathing tube bifurcate, short, representing only 8–10% of total body length. Posterior spiracles brown,



Figs. 1-9. *Typopsilopa nigra*. 1, Egg, dorsal view. 2, Cephalopharyngeal skeleton, first instar. 3, Third instar, dorsal view. 4, Same, facial mask, ventral view. 5, Same, anterior spiracle. 6, Same, perianal pad, ventral view. 7, Same, posterior spiracle. 8, Same, cephalopharyngeal skeleton. 9, Puparium, dorsal view. Abbreviations: A, antenna; AS, anterior spiracle; C, cephalic segment; DC, dorsal cephalic cap; PS, posterior spiracle; S, sensillum. Scale bars = 0.5 mm.

glabrous; spiracular scar subcircular, not well defined; three spiracular openings on spiracular plate, each oblate, two adjacent to each other with similar orientation, third positioned away and oriented nearly perpendicular to first two; spiracles each with five interspiracular processes (float hairs), each process with 2-3 branches (Fig. 7). Cephalopharyngeal skeleton darkly pigmented; paired mouthhooks crescent-shaped, pointed, with approximately 12-15 minute accessory teeth; ligulate sclerite subtriangular; hypopharynx and parastomal bar not discernible from each other; lateral pharyngeal bridge rounded and inconspic-

uous in lateral view; dorsal bridge projecting in lateral view; dorsal cornu narrow with large posterior window; ventral cornu 2× width of dorsal cornu, tapering to lightly pigmented point posteriorly, mediadorsal projection present with small window (Fig. 8).

Puparium.—Length 3.98-4.48 mm (\bar{x} = 4.17); maximum width 0.92-1.24 mm (\bar{x} = 1.12) (Fig. 9). Uniformly amber, slightly arcuate in lateral view, ovoid in dorsal view, widest near center. Anterior spiracles project laterad, posterior spiracles and breathing tube similar to third instar. Dorsal cephalic cap with peripheral carina; flat, gla-

brous. Pupa visible through translucent integument.

Biology and Larval Feeding Habits

Larvae of the noctuid moth *Bellura obliqua gargantua* create nearly linear tunnels along the length of bulrush and cattail stems that are lined with decaying plant tissue and frass. Feeding larvae produce an entrance hole approximately 6–8 mm in diameter exposing the tunnel to the environment, and thus allowing adults of *T. nigra* to oviposit at a food source appropriate for their saprophagous larvae. Little adult behavior was noted in the field. Most individuals were seen on the vertical stems of bulrush and cattail facing downwards. Adults were apparently more common in areas of dense cattail growth than bulrush. The small flies were not wary, and most scurried to the other side of the plant they were resting on if approached too closely. When disturbed, they flew only short distances, usually to neighboring plants. Several adults were observed feeding at semi-liquid bird droppings deposited on plant stems. These adults gave way to larger flies such as *Sepedon pacifica* Cresson (Sciomyzidae) and *Ceroxys latiusculus* (Loew) (Otitidae) that also congregated at the droppings, but returned shortly to feed again.

Typopsilopa nigra adults exhibited distinct courtship behavior while in laboratory breeding cages. A male perched on the side of a cage near a female would frequently sway its body in a circular pattern while its legs remained stationary. A male approached a female to gain position behind the prospective mate. A receptive female spread its wings and tilted them up approximately 45°. The male placed its forelegs on the abdomen of the receptive female, stroked her genital plate with its middle legs, and supported itself with its hind legs. The stroking behavior sometimes lasted up to five minutes. When a female was prepared, the male then protruded his genitalia to initiate copulation. Mating pairs remained in copula for only 15–30 sec. Im-

mediately afterward, the male moved to the front of the female and extended his proboscis. The female rapidly probed the male's proboscis with her own in what was apparently tropholaxis, although we never saw food material being exchanged. This lasted for up to 6 min during which time the female continually extended and retracted her proboscis while the male's remained nearly motionless. If the female moved away, the male swiftly moved to maintain his position face-to-face with the female. Tropholaxis was never observed before mating, and occurred only after copulation ended.

Oviposition was observed in a laboratory rearing cage containing moist paper towel and sections of decaying cattail. The adult moved among the stems, extending her short ovipositor to deposit eggs in protected crevices. Many eggs were recovered from the paper towel that had been laid in shallow folds or somewhat between the layers. Only a few were placed on the plastic sides of the cage.

Newly hatched larvae moved with peristaltic motions across the moistened layers of paper towel. The initial generation produced by the field-collected female was given decaying lettuce. First instars fed on this semi-liquid plant tissue and frequently burrowed under it. Larvae moved along the bottom of the petri dish articulating their mandibles and ingesting small amounts of the decayed material. The breathing tube was usually curved upwards allowing the posterior spiracles to be in constant contact with the atmosphere. The interspiracular processes were hydrophobic and prevented the submersion of the spiracles into the thin film of liquid. Larvae that burrowed into the plant tissue frequently kept the posterior spiracles exposed which allowed respiration to continue while concealed. Occasionally, larvae folded their posterior spiracles allowing the hydrophobic hairs lining them to be submerged as well; they did not remain fully submerged for longer than a few minutes before pushing the posterior spiracles

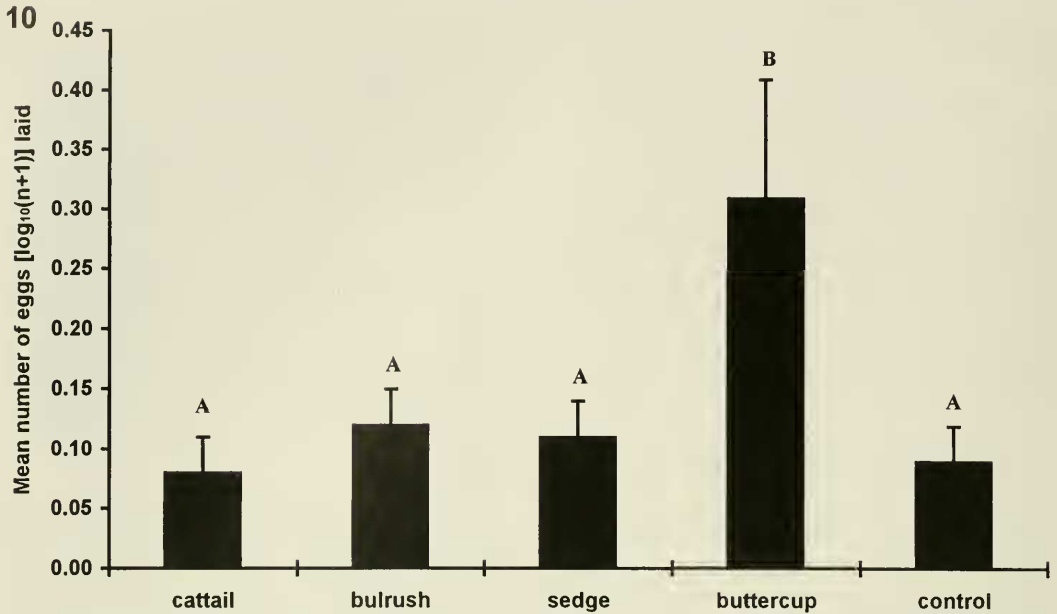


Fig. 10. Mean (± 1 SE) number of eggs (data $\log_{10}[n+1]$ transformed) laid on each substrate offered during choice experiment. Means that share letters are not significantly different.

cles above the semi-liquid material. One first instar which had died shortly after eclosion was devoured by a conspecific that encountered the carcass. However, there was no evidence of significant cannibalism, and this was probably a case of a scavenging larva taking advantage of a protein-rich food source.

Second and third instars fed at the surface of the decaying vegetation more frequently than the first instars. These older larvae occasionally moved to relatively intact material and rasped at the surface with their mouthhooks. When dishes were illuminated with a light source for observation, larvae feeding in an exposed area burrowed under the material suggesting that they are negatively phototactic. This behavior may be advantageous to a secondary invader if the host plant was somehow compromised exposing the larval habitat to predators and desiccation.

Third instars voided their guts prior to pupariation by expelling a dark green liquid from the anal slit. Formation of the puparium occurred within the masses of rotting

plant matter. Larvae burrowed into the vegetation and placed their anterior ends near the surface of the decaying material. During the initial stages of puparium formation, the anterior spiracles projected outward beyond the puparium; this probably facilitated respiration within the semi-liquid mass, as the spiracles projected above the decaying matter.

For individuals fed decaying lettuce under laboratory conditions, the duration of the first two stadia was 2–3 d, the third stadium lasted 3–4 d, and the pupal duration was 6–7 d. Adults were active in the field from late spring through October. Several puparia were collected during December, suggesting this is the overwintering stage. However, warm winters in the latitude of southern California and the rapid development exhibited by *T. nigra* suggests that adults may become active during successive warm days. *Typopsilopa nigra* is multivoltine in southern California; the rapid development of the immatures suggests that multivoltinism occurs in northern regions of its range.

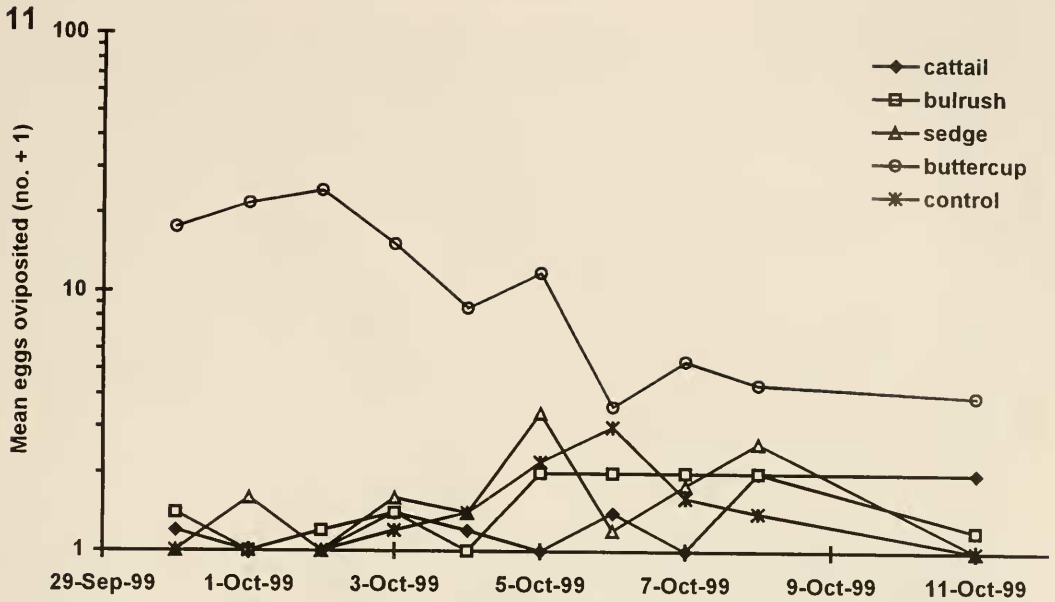


Fig. 11. Mean (n + 1) eggs laid on each substrate per day.

Laboratory reared females deposited significantly more eggs on putrifying buttercups than all other substrates ($H = 112.6$, $df = 4$, $P < 0.001$; Fig. 10). The mean number of eggs laid on buttercups was highest at the beginning of the experiment, and declined steadily as time progressed; mean oviposition was consistently low on the other treatments (Fig. 11). Total mean egg production decreased in a linear fashion (data $\log_{10}[n+1]$ transformed, $R^2 = 0.73$) during the 12 day experiment (Fig. 12).

DISCUSSION

Typopsilopa nigra exhibits morphological adaptations for secondary invasion of plants similar to those of other scavenging dipterans (Foote and Eastin 1974, Allen and Foote 1992, Steinly 1992, Deonier 1998). The curved mouthhooks of the cephalopharyngeal skeleton appeared to aid in the maceration of decaying plant material, allowing maggots to ingest small pieces of presumably microbe-encrusted organic matter. There was a distinct lack of strong spines on the integument of *T. nigra*, particularly on the creeping welts. Movement

within a narrow lepidopteran tunnel may be hampered by any strong projections which may become snagged. Larvae frequently reversed direction while moving through masses of rotting vegetation, a behavior that may not be possible in confined spaces with a strongly adorned integument.

It has been postulated that saprophagous dipteran larvae obtain their nutrition from the microbial flora associated with their food substrates (Cooper 1960, Ferrar 1987, Allen and Foote 1992). Decaying cattail and bulrush as well as lepidopteran frass are the natural larval substrates for *T. nigra*, but the actual food source supplying the energy and nutrient requirements may be the complex of bacteria, yeast, and fungi associated with rotting materials. Adults were rarely collected from stands of other wetlands plants such as buttercups, smartweeds, and sedges, and damaged areas of these plants never harbored *Typopsilopa* larvae. Nevertheless, larvae developed quickly on plant material (decaying lettuce) which is not available to them in nature. These observations suggest that adults are somewhat specific in their ovipositional preferences

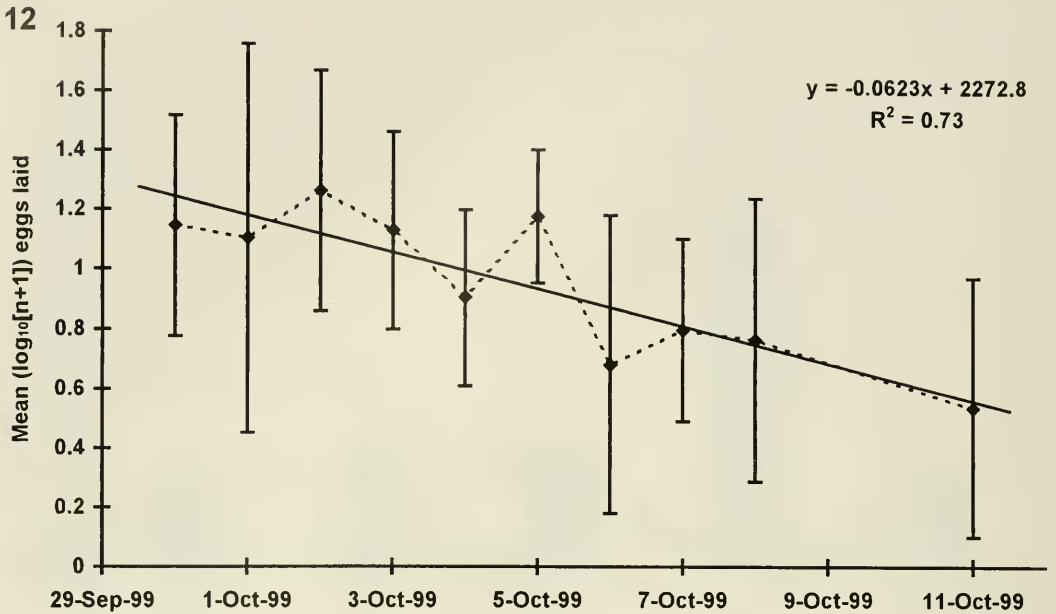


Fig. 12. Total mean (± 1 SD) egg production (data $\log_{10}[n + 1]$ transformed) per day ($-\diamond-$) with regression line added ($-\text{---}$).

(using damaged bulrush and cattails only), whereas the larvae are more generalized in their food substrate requirements.

It is surprising that significantly more eggs were laid on the decaying buttercups than on the other substrates offered during the oviposition experiment. Shredded buttercups liquefied after several days of decay and formed a semi-liquid substrate. In the confines of the experimental cages, females may have selected the buttercups as an oviposition site because of the increased moisture. The interior of cattail and bulrush plants damaged by *B. o. gargantua* was always moist, and the mixture of decaying plant matter and lepidopteran frass frequently generated a wet substrate. In nature, phytophagous insects are attracted to host plants by a variety of volatile chemicals (Price 1997), and parasitic insects locate hosts within plants using chemical cues produced by damaged plant tissue or frass (e.g., DeMoraes et al. 1998, Pare and Tumlinson 1998, Rose et al. 1998). The elucidation of the cues that *T. nigra* use to select bulrush and cattails as "host plants" will

help explain the apparent host specificity exhibited by this species as well as other dipteran secondary invaders.

Larval *T. nigra* have probably experienced few selective pressures affecting their foraging behavior and trophic ecology. In nature, they hatch from eggs deposited in an enclosed area (a tunneled plant), and lack dispersal capabilities due to their small size and inability to withstand desiccation. Other saprophagous ephydriids such as *Discocerina* spp. consume a wide variety of decaying materials in wet situations, and their larvae also are adorned with interspiracular processes on the posterior spiracles which act as float hairs (Foote and Eastin 1974); this adaptation is essential for respiration in aquatic and semiaquatic environments. It is probable that the ancestral species of *Typopsilopa* were preadapted for existence within the semi-liquid medium of rotting plant tissue, and natural selection has acted more heavily on adult ovipositional behaviors than on larval feeding habits.

It has been proposed that the food source

for ancestral dipterans was rotting vegetable matter (Oldroyd 1964, Ferrar 1987). *Typopsilopa* is considered a relatively primitive genus within the subfamily Hydrelliinae, according to recent classification schemes (Zatwarnicki 1992, Mathis and Zatwarnicki 1995). Certain members of this subfamily utilize plants for respiration (e.g., *Notiphila*) or are leaf miners (e.g., *Hydrellia*). Based on these systematic data and the assumption that the ancestral larvae were generalized scavengers, we hypothesize that *Typopsilopa* represents an evolutionary stepping stone along the progression from scavenger to herbivore in the Hydrelliinae. Ancestral adults were probably generalized in their oviposition behaviors and deposited eggs in masses of decaying vegetation. Those individuals specialized at oviposition within damaged areas of plants (e.g., bulrush and cattails) and ultimately within exposed lepidopteran tunnels had offspring that may have faced reduced selection pressures such as predators and climatic stress. Herbivorous species or genera of Hydrelliinae may have arisen from species whose larvae were saprophagous but whose adults were relatively host specific in their ovipositional preferences.

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